Ecosystems (2014) 17: 1384–1396
DOI: 10.1007/s10021-014-9801-5

ECOSYSTEMS

Elephant (*Loxodonta africana*) Disturbance to Riparian Woodland: Effects on Tree-Species Richness, Diversity and Functional Redundancy

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ABSTRACT

The substantial increase in elephant populations across many areas in southern Africa over past decades is prompting concerns about the effects on biodiversity. We investigated the outcomes of elephant disturbance on tree-species presence, density, and richness, and on alpha and beta diversity within riparian woodland in Chobe National Park, Botswana. We enumerated all tree species occurring in 32 plots (0.06 ha) along the Chobe riverfront. Plots were stratified by soil type (nutrient-rich alluvium vs. nutrient-poor Kalahari sand covering alluvium) and elephant impact (high vs. low impact on both soil types). We tested four predictions: elephants reduce tree density, richness, and alpha diversity; beta diversity is greater in vegetation subjected to high elephant impact; elephant impact on tree-species composition is greater on nutrient-poor than on nutrient-rich soil; and the loss or decline of abundant tree species on heavily disturbed sites is offset by an increase in abundance of functionally similar species, ones that are minor on lightly disturbed sites. Elephant browsing substantially affected tree-species composition, reducing density, species richness, evenness, and alpha diversity but had no effect on beta diversity. The dominant species on relatively undisturbed areas were partly replaced by functionally similar species on heavily disturbed sites. Soil type influenced species composition on lightly disturbed sites but was less important at higher elephant densities. Our findings are important for areas with extreme dry-season densities of elephants but should not be extrapolated to infer purported effects of elephants on tree diversity at lower densities.

Key words: beta diversity; ecosystem function; species dominance; Chobe; elephants; *Loxodonta africana*; resilience; ecological distance; riparian woodland.

INTRODUCTION

Several studies have suggested that biodiversity influences aspects of ecosystem functioning (for example, Hooper and others 2005; Naeem and others 2009), and that the loss of individual species

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Received 24 December 2013; accepted 1 July 2014;

Electronic supplementary material: The online version of this article (doi:10.1007/s10021-014-9801-5) contains supplementary material, which is available to authorized users.
Author Contributions LPR and SRM designed the study, carried out the statistical analyses and co-wrote the paper; LPR undertook the field work and initial data analysis.
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or groups can reduce an ecosystem's capacity to retain important functions (Mori and others 2013). The most abundant primary producers, often termed foundation species, are important for ecosystem processes through regulating population and community dynamics (Ellison and others 2005). Any ecosystem comprises a few common and many less abundant species, irrespective of taxa (McGill and others 2007). Following severe disturbance, the relative abundance of these species often changes, with previously minor species becoming more common as abundant species decline (for example, Walker and others 1999; Synnos and Arnott 2013). One hypothesis is that some minor species can play similar functional roles in the ecosystem to previously more abundant species, but their tolerance of disturbance often differs (Mori and others 2013). When they do, ecosystem function will remain even if the abundant species are lost. Because of this functional redundancy (Walker and others 1999), a species-rich ecosystem will be more resilient than one that is species-poor. These minor species accordingly have the potential to play an insurance role against major perturbations (Yachi and Loreau 1999).

More recent studies have focused increasingly on functional groups rather than individual species. These are assemblages of species with similar functional traits, that is, phenotypic features that determine an individual's effect on or response to ecosystem functioning. The variation or dispersion of functional traits in a given assemblage then represents functional diversity (Mori and others 2013 and references therein).

The link between ecosystem functioning and the roles played by abundant species is an important element in ecosystem management and conservation (Walker 1992, 1995; Risser 1995; Naeem 1998; Peterson and others 1998; Walker and others 1999). Abundant species within a life form should be functionally different (Walker and others 1999) given that they occupy different environmental or perturbation niches in the system (Pielou 1975; Huston 1994). Accordingly, the number of different functional groups reflects the number of different ecological functions performed within an ecosystem (Peterson and others 1998), with this functional diversity imparting resilience to an ecosystem undergoing environmental change (Mori and others 2013).

In African savannas, herbivory by elephant (*Loxodonta africana*), along with fire and drought, are considered to be the primary disturbances structuring woodlands (Lewis 1991; Ben-Shahar 1993; Levick and Asner 2013). All can change the system from one state to another (van de Koppel and Prins 1998; Holdo and others 2009). In northern Botswana, the elephant population has increased by 6% per annum since 1987 (DWNP 1997; Gibson and others 1998; Chase 2011; DWNP 2013), with recent population estimates varying between 128,000 (Chase 2011) and 208,000 (DWNP 2013). Previous studies have raised concerns over the effects of elephants on biodiversity (Dickson and Adams 2009; Smit and Ferreira 2010; van Wilgen and Biggs 2011; Levick and Asner 2013), but studies are few, and information is lacking (Kerley and others 2008). In northern Botswana, intense elephant browsing has been reported to be the main disturbance along the Chobe riverfront, converting tall-canopy riparian woodland to shrubland (Mosugelo and others 2002), and potentially changing species richness, composition, and the number of functional groups, with possible adverse consequences for ecosystem functioning. According to the insurance hypothesis outlined above, functional redundancy will mitigate major perturbations such as this (see Mori and others 2013 for a review), but whether such redundancy exists, either in this savanna system or any other experiencing increased elephant numbers, is as yet unknown.

Large browsers such as elephants typically create spatial variation in plant structure and species composition (for example, Nellemann and others 2002) because of their spatially concentrated browsing patterns. These can be attributed to several interacting factors, particularly spatial variations in water availability and soil nutrients which in turn affect plant species composition and palatability (du Toit and others 2014). Soil in particular is considered to be important in regulating elephant browsing in northern Botswana (Skarpe and others 2014a).

Although large parts of the riparian woodland along the Chobe River have been converted to shrubland, pockets of relatively undisturbed areas remain (Mosugelo and others 2002), thereby providing an opportunity to study the effects of elephant browsing on species richness, diversity, and functional redundancy.

Our hypothesis that the activities of elephant populations affect functional redundancy and ecosystem resilience by altering woody plant species composition, diversity, and heterogeneity, leads to four predictions: (1) elephants reduce tree density, richness, and alpha diversity in the Chobe riparian woodland; (2) beta diversity is greater in vegetation subjected to high elephant impact; (3) elephant impact on tree species composition is greater on nutrient-poor than on nutrient-rich soil; and (4) the loss or decline of abundant species on sites where elephants have transformed riparian woodland to shrublands or mixed woodland (heavily disturbed sites) is offset by an increase in abundance of functionally similar species, ones that are minor in the remnant riparian woodlands (lightly disturbed sites).

Methods and Materials

Study Area

The study was conducted within Chobe National Park in northern Botswana, focused on a 20-km-long strip of riparian woodland along the Chobe River, from the eastern boundary of the Chobe National Park (17°81′S, 25°15 E) to the old Serondela tourist campsite (17°84′S, 25°84′ E). The Chobe River forms the international boundary between Botswana and Namibia. The riparian woodland previously formed a continuous dense canopy along the Chobe River, but it has been gradually fragmented, and now only remnants of the once-continuous belt of tall mature trees remain in lightly disturbed areas (Simpson 1975; Mosugelo and others 2002). These remnants are typically associated with areas avoided by elephants because of proximity to houses and campsites or with steep slopes inaccessible to elephants. Where elephant disturbance has been heavy, woodland cover has been reduced. Although several factors could have contributed to this loss of riparian woodland, the increasing numbers of elephants are considered to be the main agent of change (Child 1968; Simpson 1975; Sommerlatte 1976; Moroka 1984; Mosugelo and others 2002). Most congregate along the riverfront during the dry season, because the river is the only source of water (Skarpe and others 2014a). During the rainy season, most herbivores move south into *Baikiaea plurijuga* woodland and concentrate around seasonal pools and pans. Apart from elephants, common herbivores in the area include greater kudu (*Tragelaphus strepsiceros*), impala (*Aepyceros melampus*), hippopotamus (*Hippopotamus amphibius*), giraffe (*Giraffa camelopardalis*), roan (*Hippotragus equinus*), sable (*H. niger*), and waterbuck (*Kobus ellipsiprymnus*).

Soils in the study area can be grouped into two distinct classes: nutrient-poor Kalahari sand (Ben-Shahar and MacDonald 2002); and more fertile clay-rich alluvium representing old floodplain deposits (Simpson 1975). Annual rainfall is about 600 mm (MDS 2001), concentrated from November to May when most of the plant growth takes place (Omphile 1997). Temperatures range from 6 to 34°C with June and July being the coldest months and September–November the hottest (Omphile 1997).

Vegetation Sampling

A total of 32 20 m × 30 m plots were laid out systematically along the Chobe riverfront, 16 on heavily disturbed sites and 16 on lightly disturbed sites (Mosugelo and others 2002). Eight of the plots on heavily disturbed sites were positioned in areas where the alluvium is covered with nutrient-poor Kalahari sand (termed sand, heavily disturbed, SHD); the other 8 were located on pure alluvium, a more nutrient-rich substrate (alluvium, heavily disturbed, AHD). Likewise, in lightly disturbed areas, 8 plots were situated on alluvium covered with Kalahari sand (sand, lightly disturbed, SLD), and the others were positioned on pure alluvium (alluvium, lightly disturbed, ALD). These four groups are our ''treatments''. In each plot, all woody plants were identified and recorded. To describe vegetation structure, the height of each individual woody plant was recorded using either a Suunto tree-height meter, to measure tall trees, or a measuring tape to measure small ones. Woody plants were categorized into five height classes (small shrubs, <1 m; shrubs, 1–3 m; small trees, 3–5 m; trees: 5–10 m; and large trees, >10 m).

Diversity and Community Similarities

We used Rényi profiles for diversity comparisons, because arbitrary selection of a diversity index can give conflicting results, and the Rényi profile is robust against such cases (Kindt and Coe 2005). The profiles also provide information on species richness (sites with high values for alpha = 0 have high richness) and evenness (horizontal profiles indicate greater evenness than less horizontal profiles).

Beta diversity, within-treatment species heterogeneity (Anderson 2006; Anderson and others 2006), was determined using the function *betadisper* in Vegan in R (Oksanen and others 2012). In our study, beta diversity is the species heterogeneity among plots within our four treatments (that is, SLD, SHD, ALD, and AHD). Tukey's HSD was used as a post-hoc test to evaluate pair-wise contrasts between these groups.

To compare the tree-species compositional similarities between disturbance and soil categories, we calculated generalized Morisita's similarity indices (C_m) using abundance data to compare multiple assemblages (Chao and others 2008; Jost 2008). We estimated 95% confidence intervals from 200 bootstrap replications, using the free software SPADE (http://chao.stat.nthu.edu.tw/software/SPADE/SPADE_UserGuide.pdf).

Species Attributes

Determining the functional relationships among plant species is problematic in the sense that knowledge of so-called 'hard' attributes, such as growth and transpiration rates and levels of nutrient release, is needed (Walker and Langridge 2002). Information on these parameters is generally lacking for African tree species. Instead, we used available information on 'soft' attributes, such as leaf area and plant size, as surrogates (Walker and Langridge 2002), following Skarpe (1996) and Walker and others (1999). We selected five attributes that we considered important for assessing the effects of elephant disturbance on vegetation. *Average height at maturity* was chosen, because a tree's height influences its ability to compete for light, resist wind, and support leaves and chemical transport (Westoby 1998). It also influences elephant feeding and the extent to which an elephant will impact individual trees. *Leaf area* affects light absorption, heat balance, and the diffusion of water and carbon dioxide (Orians and Solbrig 1977). It is also significantly positively correlated with tree mass and relative growth rates (Porter and Remkes 1990) and with herbivore feeding preferences, because fast-growing trees generally have low levels of anti-herbivore metabolites (Coley and others 1985). *Growth form* affects how much biomass is available to herbivores and the response to herbivory (Skarpe 1996). *Leaf life span* is determined by a species' response to climatic variations (Skarpe 1996). *Fruit type* influences a tree's mode of dispersal and its dispersibility, which in turn affects a species' colonization and regeneration ability. Information on these attributes was obtained from the southern African literature (van Wyk and van Wyk 1997; Roodt 1998; Palgrave and Palgrave 2002). Some potentially important attributes such as ability to coppice, response to removal of biomass, root type, seed mass, and palatability are not well documented and therefore were not included here. Following Walker and others (1999), the attributes were standardized on a scale of 1 to 5 for comparisons (Appendix 1 in Supplementary Material). Species' scores for each attribute are shown in Appendix 2 in Supplementary Material. Although Walker and others (1999) tested their hypotheses on the effects of livestock grazing on graminoids, the same methods can be used to study the effects of elephant browsing on woody plants. Using a combination of historical information (for example, Chapman 1868; Selous 1881; Schulz and Hammer 1897; Pole-Evans 1948; Hodson 1987), studies conducted in the study area (for example, Child 1968; Simpson 1975; Moroka 1984; Mosugelo and others 2002), and that lightly disturbed sites are associated with human settlements and campsites inside the park, rather than inherent differences in vegetation, we assume that the species composition of heavily disturbed sites was once identical to lightly disturbed sites before elephant disturbance.

Ecological Distances and Species Abundance

Many indices have been proposed to measure ecological dissimilarities. The simplest is Euclidean distance or ecological distance (ED), which measures the differences among species for an attribute in abstract space. EDs between all species pairs were calculated, and groups representing apparent clusters were selected (following Walker and others 1999). We used the simplified version of ED

$$\mathrm{ED_{jk}} = \sum \left(A_{ij} - A_{ik}\right)^2$$

where $\mathrm{ED_{jk}}$ is the ED between species j and k, and A_{ij} and A_{ik} are values of species j and k for attribute i. This measure of functional attribute diversity is similar to Rao's quadratic entropy (Rao 1982) but differs in how the distance matrix is calculated (Schleuter and others 2010).

On each plot species, abundances were ranked, and their relative proportion to total abundance was determined. Species that contributed two-thirds of the relative abundance on each plot were considered to be abundant. The EDs for all species on each plot were calculated and summed for each site (disturbed and intact sites separated in turn by soil types). The EDs for abundant species were compared with the average EDs within sites. We expected large EDs between co-abundant species. Assuming that species recorded on lightly disturbed sites were present on heavily disturbed sites prior to elephant impact, we employed differences in relative abundances between these sites on each soil type to determine if a species had increased or decreased under disturbance, using Walker and others' (1999) definitions and approach.

We used analysis of variance to test if the density of trees in the various size classes differed between soil types and levels of elephant disturbance. A Fisher's exact test for homogeneity was performed to test frequencies, by sites, between abundant species and all species on sites. The same test was used to test functional similarities between decreasing species and increasing species across soil type.

RESULTS

Density, Diversity, and Community Similarities

Overall tree density was three times higher on lightly disturbed sites compared with heavily disturbed sites on Kalahari sand but did not differ with disturbance on alluvium (Table 1). Only the densities of small shrubs on both soil types were significantly lower on heavily disturbed sites compared with lightly disturbed ones. Densities of small trees and trees did not differ between heavily and lightly disturbed sites on either soil type (Table 1).

Twenty-nine tree species from 18 families were recorded in the study area (Appendix 2 in Supplementary Material). Species richness declined as elephant disturbance intensity increased, particularly on the relatively nutrient-poor Kalahari sand sites (Figure 1). High elephant disturbance also correlated negatively with alpha diversity on both alluvium and Kalahari sand (Figure 1). Although alpha diversity was higher on lightly disturbed sand than on lightly disturbed alluvium, alpha diversity did not differ between alluvium and Kalahari sand of heavily disturbed vegetation.

Beta diversity was not correlated with elephant disturbance (Figure 2). Sites on Kalahari sand had significantly lower beta diversity than those on alluvium (Tukey multiple comparison tests, $P < 0.02$) but were not correlated with elephant disturbance within soil types (Tukey multiple comparison tests, $P > 0.87$).

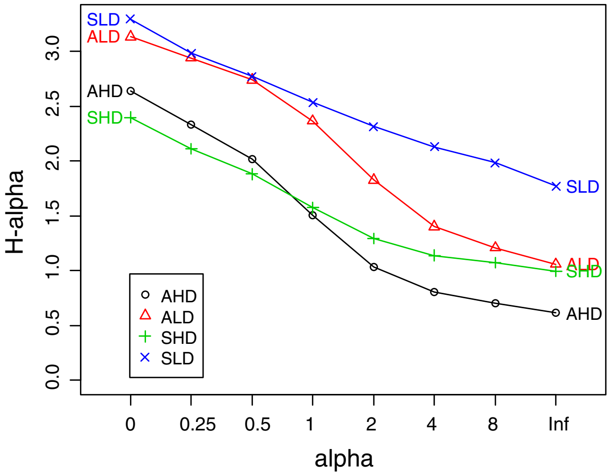

Figure 1. Rényi plots of the different disturbance and soil categories: *SLD*, sand lightly disturbed; *SHD*, sand heavily disturbed; *ALD*, alluvium lightly disturbed; *AHD*, alluvium heavily disturbed. Profiles with higher H-alpha have high diversity. Crossing curves cannot be differentiated in terms of diversity (that is, SLD > ALD > SHD = AHD). Species richness is given at alpha = 0, ($e^{\text{H-alpha}}$).

Lightly disturbed areas on both sand and alluvium had low species similarities (Morisita similarity index, C_m, 0.44: Table 2), in contrast to the much greater similarity among species between heavily disturbed areas on sand and alluvium ($C_m = 0.72$). Species similarities were the lowest between the lightly disturbed areas on sand and the heavily disturbed areas on alluvium ($C_m = 0.31$), and moderately high between the lightly and

Table 1. Comparison of Woody Plant Density (All Tree Species Combined) on Lightly Disturbed and Heavily Disturbed Sites Along the Chobe Riverfront, Northern Botswana

Group	Alluvial soil covered with Kalahari sand			Alluvial soil		
	Lightly disturbed sites Mean (SE)	Heavily disturbed sites Mean (SE)	*P*	Lightly disturbed sites Mean (SE)	Heavily disturbed sites Mean (SE)	*P*
Density						
Small shrubs (<1 m)	0.687 (0.070)	0.160 (0.070)	<0.001	0.170 (0.030)	0.020 (0.030)	0.002
Shrubs (1–3 m)	0.070 (0.010)	0.050 (0.010)	0.360	0.030 (0.010)	0.020 (0.010)	0.120
Small trees (3–5 m)	0.007 (0.003)	0.014 (0.003)	0.180	0.005 (0.003)	0.011 (0.003)	0.290
Trees (5–10 m)	0.005 (0.002)	0.007 (0.002)	0.830	0.003 (0.002)	0.005 (0.002)	0.320
Large trees (>10 m)	0.004 (0.001)	0.002 (0.001)	0.260	0.004 (0.001)	0.002 (0.001)	0.120
Overall	0.150 (0.020)	0.050 (0.020)	0.040	0.040 (0.020)	0.050 (0.020)	0.770

Probability values from ANOVA.

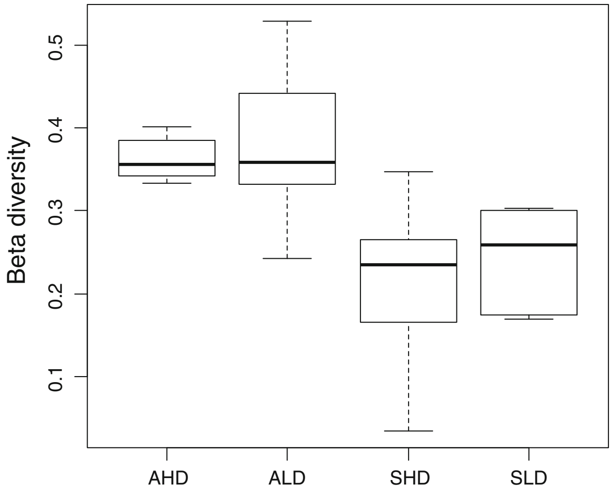

Figure 2. Beta diversity (within-group heterogeneity) for the different disturbance and soil categories (see Figure 1 for notations).

heavily disturbed alluvium sites (C_m = 0.60: Table 2).

Functional Redundancy

The species abundance distributions were dominated by only a few species on the heavily disturbed sites compared with less disturbed sites (Figures 1, 3). Five out of 23 species on lightly disturbed alluvium and eight out of 22 species on lightly disturbed sand accounted for two-thirds of tree abundance on these sites. In contrast, on the disturbed sites, only two species made up this fraction, out of 13 and 12 species overall on heavily disturbed alluvium and heavily disturbed sand, respectively (Figure 3). The species concerned were *Croton megalobotrys*, which accounted for more than 50% of total abundance on heavily disturbed alluvium, and *Capparis tomentosa* on the disturbed alluvium sites and *Combretum mossambicense* on heavily disturbed sand (Figure 3). Elephant-disturbed areas seem to be associated with few functional groups, principally fast-growing deciduous species such as *C. megalobotrys* and *Combretum mossambicense*.

More than two-third of the minor species were functionally similar to the abundant species in the lightly disturbed sites on both soil types: 12 out of 14 species (86%) on Kalahari sand; 13 out of 18 species (72%) on alluvium. In contrast, in heavily disturbed sites on both soil types, less than one-third of the minor species were functionally similar to the abundant ones: three out of 10 species (30%) on Kalahari sand; three out of 11 species (27%) on alluvium.

Mean ED for all woody species pairs on the Chobe riparian woodland was 18.8 (Appendix 3 in Supplementary Material). We divided the frequencies of EDs between species pairs into five clusters (Appendix 4 in Supplementary Material). *Functionally similar species* were taken to be those with EDs $\leq$ 7 (17% of all pair-wise comparisons); *similar to average species* had EDs 8 $\leq$ 15 (25% of all pair-wise comparisons); *average species*: ED 16 $\leq$ 23 (27%); *average to dissimilar species*: ED 24 $\leq$ 32 (16%); and *functionally dissimilar species* with EDs $\geq$ 33 (15% of all pair-wise comparisons).

On lightly disturbed alluvium, functional similarity among the abundant species did not differ significantly from the site average (Fisher's exact test, $P = 0.22$; Table 3). In contrast, on lightly disturbed sands and on the heavily disturbed sites on both soil types, the abundant species were functionally more similar than the site average (Fisher's exact test: for lightly disturbed sands, $P = 0.008$; for heavily disturbed sites, $P < 0.001$ in both cases; Table 3). On Kalahari sand, six out of the eight dominant species on the lightly disturbed sites (75%) declined in abundance on heavily disturbed sites (Table 4). Of these six decreasing species, only three were replaced by an increase in abundance of functionally similar minor species, a non-significant replacement (Fisher's exact test, $P > 0.05$,

Table 2. Moristia Species Similarity Indexes for Combinations of Elephant Disturbance and Soil Nutrient Levels

Pair-wise comparisons	Estimate (±SE)	95% Confidence intervals
SLD versus SHD	0.387 (0.019)	0.350–0.424
SLD versus ALD	0.437 (0.034)	0.371–0.503
SLD versus AHD	0.307 (0.020)	0.268–0.346
SHD versus ALD	0.448 (0.048)	0.354–0.543
SHD versus AHD	0.717 (0.037)	0.644–0.791
ALD versus AHD	0.595 (0.060)	0.477–0.712

SLD, sand, lightly disturbed; SHD, sand, heavily disturbed; ALD, alluvium, lightly disturbed; AHD, alluvium, heavily disturbed.

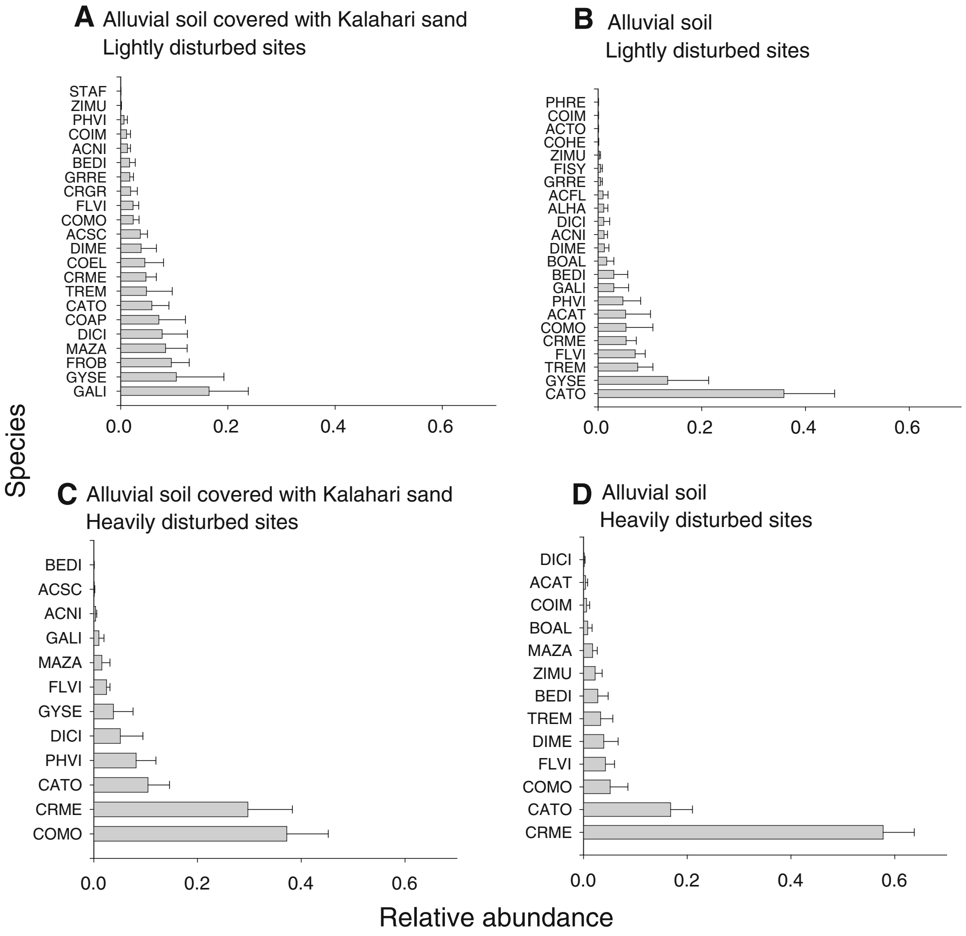

Figure 3. Relative abundances (number of stems/km^2 and SE) of woody plant species in different sites and soil types along the Chobe riparian woodland, northern Botswana. The figure is re-drawn from Moe and others (2014) with permission from Wiley-Blackwell. *ACSC, Acacia schweinfurthii*; *ACFL, Acacia fleckii*; *ACNI, Acacia nigrescens*; *ACTO, Acacia tortilis*; *ALHA, Albizia harveyi*; *BEDI, Berchemia discolor*; *BOAL, Boscia albitrunca*; *CATO, Capparis tomentosa*; *COAP, Combretum apiculatum*; *COEL, Combretum elaeagnoides*; *COHE, Combretum hereroense*; *COIM, Combretum imberbe*; *COMO, Combretum mossambicense*; *CRGR, Croton gratissimus*; *CRME, Croton megalobotrys*; *DICI, Dichrostachys cinerea*; *DIME, Diospyros mespiliformis*; *FISY, Ficus sycomorus*; *FLVI, Flueggea virosa*; *FROB, Friesodielsia obovata*; *GALI, Garcinia livingstonei*; *GRRE, Grewia retinervis*; *GYSE, Gymnosporia senegalensis*; *MAZA, Markhamia zanzibarica*; *PHVI, Philenoptera violacea*; *PHRE, Phyllanthus reticulatus*; *STAF, Sterculia africana*; *TREM, Trichilia emetica*; *ZIMU, Ziziphus mucronata*.

Table 4). Of the five dominant species on lightly disturbed alluvial soils, only one, *Gymnosporia senegalensis*, was less abundant on the heavily disturbed sites (Table 4). Based on the criteria used in this study, the decrease in abundance of *G. senegalensis* was offset by increases in abundance of functionally similar species (*Markhamia zanzibarica* and *Ziziphus mucronata*) on heavily disturbed sites relative to their abundance on lightly disturbed sites (Table 4).

Discussion

Tree densities overall were higher on lightly disturbed sites than on heavily disturbed sites. The most pronounced difference was in the high density of small shrubs (<1 m) on the less impacted areas of both soil types. Stokke and du Toit (2000) reported that elephants in the same study area browsed predominantly between 1 and 3 m, in line with findings in other African woodlands (predominant browse range 1–5 m: Croze 1974; Belsky 1984; Pellew 1984; Jachmann and Bell 1985). While elephants do not commonly browse below 1 m, medium-sized impala feeds extensively on seedlings (du Toit 1990; Rutina and others 2005). Indeed an experimental study in the same area found that impala was the most important seedling consumer (Moe and other 2009). Elephant browsing can facilitate ungulate browsing (Barnes

Table 3. Percent of Pair-Wise Comparisons of EDs for All Species and for Abundant Species Occurring in Each Functional Similarity Class at Each Site

Functional similarity of pairs	Kalahari sand covering alluvium				Alluvial soil			
	Lightly disturbed sites		Heavily disturbed sites		Lightly disturbed sites		Heavily disturbed sites	
	All species (%)	Abundant species (%)	All species (%)	Abundant species (%)	All species (%)	Abundant species (%)	All species (%)	Abundant species (%)
Similar	18	38	19	50	12	7	6	32
Similar to Average	28	25	18	5	25	25	24	6
Average	23	9	34	5	33	47	41	12
Average to dissimilar	17	16	23	35	16	13	19	45
Dissimilar	14	12	6	5	14	8	10	5
Probability	$\chi^2 = 13.62$, $P = 0.008$		$\chi^2 = 45.41$, $P < 0.001$		$\chi^2 = 5.71$, $P = 0.220$		$\chi^2 = 59.65$, $P < 0.001$	

1996; van de Koppel and Prins 1998; Rutina and others 2005), and opening up the canopy by elephants along the Chobe Riverfront (Mosugelo and others 2002) has been associated with an increase in browsing ungulates such as impala (Rutina and others 2005). In other African woodlands, impalas have been reported to retard regeneration of trees (Prins and van der Jeugd 1993; O'Kane and others 2012; Støen and others 2013), and the same perhaps is happening in Chobe (Moe and others 2009, 2014).

Woody species richness declined substantially with elephant disturbance intensity. Alpha diversity was the highest on the lightly disturbed sands and was also higher on lightly disturbed alluvium than in heavily disturbed areas. Although soil type apparently influenced alpha diversity in lightly disturbed areas, this influence was not evident on heavily disturbed sites where diversity between the two soil types was similar.

This supports our first prediction that elephants reduce woody species density, richness, and alpha diversity. During the dry season, elephant densities along the Chobe riverfront can be as high as 20 elephants km^{-2} (Teren and Owen-Smith 2010), and this has resulted in opening up the woodland here (Mosugelo and others 2002). These changes, however, are only visible within 2–3 km of the Chobe River (Mosugelo and others 2002). In more central areas of the Chobe National Park, elephant impacts were more limited, primarily an increase in tree density, cover, and volume caused by a combination of increasing numbers of trees in the smaller size classes and a decrease in larger trees (Kalwij and others 2010).

Our second prediction that elephants-increased beta diversity (that is, within habitat heterogeneity) was not supported. Beta diversity was low in the areas where Kalahari sand overlaid alluvium compared with the more nutrient-rich pure alluvium, but beta diversity was not associated with elephant impact. Previous studies have shown how large herbivores, particularly elephants, can increase vegetation heterogeneity (for example, Kohi and others 2011; Fornara and du Toit 2007), but these often refer to larger areas where elephants create a mosaic of habitats through spatial differences in browsing pressure (Nellemann and others 2002). Our study shows that there was no evidence that elephant impact tree diversity when measured on a smaller scale and confined to distinct vegetation types, although structural heterogeneity can still change. In this case, beta diversity might relate more to differences in abiotic factors like soil nutrients. Although this study did not find any

Table 4. Functional Similarities Between Decreasing and Increasing Woody Plant Species Following Elephant Browsing along the Chobe Riverfront, Northern Botswana

Kalahari sand covering alluvium			Alluvial soil		
Decreasing species	Functionally similar increasing species	ED	Decreasing species	Functionally similar increasing species	ED
Acacia schweinfurthii	None	–	*Acacia schweinfurthii*	None	–
Acacia nigrescens	*Croton megalobotrys*	6	*Acacia nigrescens*	*Croton megalobotrys*	6
Combretum apiculatum[1]	*Croton megalobotrys*	2	*Acacia tortilis*	None	–
	Combretum mossambicense	5	*Acacia fleckii*	None	–
Combretum elaeagnoides	*Croton megalobotrys*	6	*Albizia harveyi*	None	–
	Combretum mossambicense	5	*Dichrostachys cinerea*	None	–
Combretum imberbe	*Philenoptera violacea*	6	*Combretum hereroense*	*Combretum imberbe*	5
Croton gratissimus	*Croton megalobotrys)*	2		*Markhamia zanzibarica*	5
	Combretum mossambicense	5		*Ziziphus mucronata*	6
	Philenoptera violacea	5	*Gymnosporia senegalensis1*[1]	*Diospyros mespiliformis*	7
Friesodielsia obovata[1]	None	–		*Ziziphus mucronata*	6
Diospyros mespiliformis	None	–	*Garcinia livingstonei*	*Diospyros mespiliformis*	1
Berchemia discolor	None	–		*Ziziphus mucronata*	2
Garcinia livingstonei[1]	None	–	*Grewia retinervis*	None	–
Gymnosporia senegalensis[1]	*Philenoptera violacea*	3	*Philenoptera violacea*	*Croton megalobotrys*	7
	Combretum mossambicense	5	*Phyllanthus reticulatus*	None	–
Grewia retinervis	None	–	*Ficus sycomorus*	*Diospyros mespiliformis*	4
Markhamia zanzibarica[1]	*Philenoptera violacea*	6		*Combretum imberbe*	6
	Croton megalobotrys	2			
	Combretum mossambicense	1			
Trichilia emetica[1]	None	–			

[1] *Indicates species dominating on lightly disturbed sites. ED is the ecological distance between the two species. See Appendix 1, 2 and 3 in Supplementary Material for details.*

relationship between elephant browsing and the beta diversity of trees, another experimental study from Chobe has shown that large herbivores, including elephants, reduced the beta diversity of herbaceous vegetation on Kalahari sand within *B. plurijuga* woodlands (Masunga and others 2013).

Our prediction that elephants would change species composition more on nutrient-poor sites, where Kalahari sand covers the alluvium, than on pure alluvium was supported. Species similarities between the high and low elephant impacted areas were much lower (0.39 ± 0.02) on the sands than on the alluvium (0.60 ± 0.06). This could be because elephants supply nutrients in the form of dung and urine when congregating along the riverfront to drink. Input of nutrients could have a larger effect on the vegetation of nutrient-poor soils, and vegetation on these soils could be more susceptible to browsing.

Elephants substantially changed the general patterns of species similarities. While the similarity in woody species composition was relatively low (0.44 ± 0.03) between the lightly disturbed areas on sand and alluvium, it was high between these two soil types (0.72 ± 0.04) at high elephant disturbance. Thus, while soil nutrients appear to influence woody species composition when disturbance by elephants is low, species composition on the two soil types converges when subject to heavy browsing.

Our fourth prediction was not fully supported. Only some species that declined in abundance under disturbance were replaced by functionally similar species. Based on the EDs, the abundant species on lightly disturbed sites on Kalahari sand can be grouped into five functional groups, whereas the abundant species on heavily disturbed sites on sand constituted only one functional group. On the alluvial soils, abundant species on lightly disturbed sites formed four functional groups, but only two on heavily disturbed sites. On both soil types, elephant disturbance seems to have favored fast-growing deciduous woody species (mainly *C. megalobotrys* and *Combretum mossambicense*). Only the minor species on lightly disturbed sites had corresponding functionally similar abundant species. Most minor species on the heavily disturbed sites of both soil types had no matching functionally similar abundant species.

Only half of the declining species were counterbalanced by ecologically similar species when sites with Kalahari sand overlying alluvium were disturbed. In nitrogen-poor soils, such as these Kalahari sands, species that fix nitrogen (for example, legumes: Ritchie 1995) and which can competitively absorb most of the available nitrogen (Pielou 1975; Grime 1979) are expected to dominate. These species are normally rare in disturbed sites, however, because they are preferred by herbivores (Ritchie 1995). The abundant species at sites on intact Kalahari sand might therefore not have been replaced when the sites were disturbed because the functionally similar minor species were morphologically and physiologically too similar, with analogous resource needs and comparable attractiveness to herbivores. Preferred tree species are in this system constantly browsed, allowing many non-preferred species to grow to full canopy height. The opposite results were observed on alluvial soils, perhaps because of higher resource availability there. Our results suggest that there is a relationship between soil fertility and elephant browsing. Where soils are fertile, herbivory does not seem to alter much the composition of abundant plant species because their nutrient uptake is normally sufficient to compensate for losses to herbivores (Huston 1994).

Minor species have to be functionally similar to abundant species for them to maintain ecosystem functions if the populations of abundant species were to decline (Walker and others 1999). Compensation by minor species for such declines following disturbance is expected if the species within a functional group respond differently to disturbance, with some being favored and others not (Walker 1995). If all species in a functional group respond the same way, however, the whole group could be eliminated if conditions become adverse, with resulting functional loss (Walker 1995). The reduction in the number of functional groups in the heavily disturbed areas therefore might be associated with the fact that elephants are bulk feeders, impacting a broad range of tree species.

Walker and others (1999) found that abundant grasses were functionally dissimilar to each other, because they occupy different ecological niches. Later, Walker and Langridge (2002) showed that in ecosystems with mixed growth forms, abundant species were commonly functionally similar. Along the Chobe Riverfront, abundant tree species were functionally more similar than the average EDs on each site, except on lightly disturbed sites on alluvial soils. The same species of tree can have two distinctly different growth strategies. Of the 29 species along the Chobe Riverfront, 11 can alternate between tree and shrub forms. Almost half of the abundant species on each site can persist as both trees and shrubs. Tree growth form could, among other traits, determine which species would be filtered by elephant disturbance in African woodlands (*sensu* Lavorel and Garnier 2002). For example, along the riverfront heavily disturbed areas were co-dominated by *Capparis tomentosa*, *Combretum mossambicense* and *C. megalobotrys*. While *C. tomentosa* is functionally distinct from the other two species, *C. mossambicense* and *C. megalobotrys* are functionally similar (ED = 5). Elephants maintain *C. mossambicense* in a shrub growth form, and this species can therefore co-exist with the functionally similar tree, *C. megalobotrys*. Our results on functional similarities should be treated with some caution, however. Although we believe that we have selected important plant species traits for our comparisons, the traits are few and will not completely explain the ecological niche of each species.

In conclusion, this is one of the few empirical studies on the effect of elephants on biodiversity (Kerley and others 2008). While some studies have pointed to the detrimental effects of an increasing elephant population in Southern Africa (Hamandawana 2012), others have argued that elephant numbers are simply returning to levels that occurred before the great ivory hunt of the late 1800s (Skarpe and others 2014b). Some studies have found little impact of elephants on woody vegetation, even in areas with relatively high elephant densities (Kalwij and others 2010). An elephant density of about 0.5 animals km^{-2} has often been used as a rule of thumb for the onset of substantial changes in plant and animal communities (Cumming and others 1997). Our study shows that elephants can have a considerable effect on tree-species composition, density, species richness, evenness, and alpha diversity, but not on small-scale beta diversity. To some extent, the species dominating relatively undisturbed areas are replaced by functionally similar species when severely disturbed. While soil type is important for tree-species composition at low browsing pressure, it becomes less important at higher elephant densities. Nevertheless, our findings should be interpreted only in the context of the extreme dry-season elephant densities found along the Chobe River and should not be extrapolated to the effects of elephants on the diversity of trees more widely, at least until we know more about the complexities of their interactions.

ACKNOWLEDGMENTS

This study was conducted as part of the Botswana Norway Institutional Capacity Building and Collaboration Program (BONIC), jointly funded by the Department of Wildlife and National Parks (DWNP), Botswana and NORAD. J. T. du Toit, J. E. Swenson, G. Oba, R. Borgstrom and M. Tweheyo, J. Pastor and two anonymous referees improved earlier drafts of this manuscript. We are particularly grateful to Peter Frost for his substantial improvements in language and clarity. W. Marokane and M. Ramotladima helped with the identification of species in the field.

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